Aggregation dynamics explain vegetation patch-size distributions

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Abstract

Vegetation patch-size distributions have been an intense area of study for theoreticians and applied ecologists alike in recent years. Of particular interest is the seemingly ubiquitous nature of power-law patch-size distributions emerging in a number of diverse ecosystems. The leading explanation of the emergence of these power-laws is due to local facilitative mechanisms. There is also a common transition from power law to exponential distribution when a system is under global pressure, such as grazing or lack of rainfall. These phenomena require a simple mechanistic explanation. Here, we study vegetation patches from a spatially implicit, patch dynamic viewpoint. We show that under minimal assumptions a power-law patch-size distribution appears as a natural consequence of aggregation. A linear death term also leads to an exponential term in the distribution for any non-zero death rate. This work shows the origin of the breakdown of the power-law under increasing pressure and shows that in general, we expect to observe a power law with an exponential cutoff (rather than pure power laws). The estimated parameters of this distribution also provide insight into the underlying ecological mechanisms of aggregation and death.

Keywords: patch-size distribution, pattern formation, spatial ecology, aggregation

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1. Introduction

Vegetation patch-size distributions have been under intense study in recent years [1, 2, 3, 4, 5]. It has been shown that a power-law provides a good fit to the patch-size distribution under a robust range conditions, however there are marginal cases to this. Kéfi et al. [6] analysed patch-size distributions in semi-arid vegetation in the Mediterranean and found that there was not only a power-law distribution evident in the patch-size distribution, but also a truncated exponential term, when the system was under increased grazing pressure. Similar power-law distribution phenomena have also been detected in a number of other ecosystems including mussel beds [7] and marine benthic diatoms [8]. This phenomena of a power-law distribution transitioning to an exponential distribution under increasing stress has recently shown to be robust, where diverse ecological models are able to reproduce these results [2].

The leading explanation of this power-law pattern formation in ecology is due to local interactions driving the large-scale behaviour [9, 10]. Scanlon et al. [11] supported through the use of numerical simulation of spatially-explicit models of vegetation growth combined with a global effect on the population density interpreted as the amount of rainfall or other global processes. The local positive feedback process driving the patch formation is through facilitation of neighbourhood sites that increase the birth rate and decrease the death rate [5]. This explanation does not answer how a power-law forms at the patch level, whether it is due to a competition effect between larger clusters dominating the landscape or an aggregation of smaller clusters. There is also an open question of how patches aggregating together drives these observed patterns.

Models of aggregation and fragmentation have been considered in other areas in ecology such as the size of fish schools [12] and marine diatoms [13]. Aggregation phenomena has been more generally studied in the Physical sciences [14], including processes such as polymerisation [15], coagulation of aerosols [16] and flocculation [17]. Although these examples include clusters that may diffuse, aggregation phenomena may also be considered in the case where clusters are immobile [18]. Aggregation of vegetation clusters, however, has not been previously considered as an explicit driving force of the evolution of the patch-size distribution. Our novel contribution here is to apply established theory of aggregation dynamics to the system of vegetation clusters and derive a new model of aggregation with global death that

is applicable to vegetation dynamics.

In this article, spatially implicit models of vegetation clusters are investigated by considering how patches form and aggregate. The general conditions under which a power-law distribution is expected to emerge are explored as well as when there is a breakdown of the power law distribution due to an exponential truncation. By adopting a patch-centric viewpoint, the impact of aggregation on the resulting distribution along with other processes may be studied directly. This represents a powerful new approach to understanding the origin of these distributions, by explicitly modelling the patch-size dynamics without the need to infer the patch-size distribution from a spatially explicit model [5].

Further, the connection between the power-law exponent and the persistence of the distribution in this model is explored. We begin by defining a novel model of aggregation with linear death and then deriving an asymptotic solution when the death rate is small.This analytic result is compared to a simulation study of vegetation with local and global growth properties subjected to a global disturbance. For small disturbance, the power law exponent closely matches the exponent expected from the model. The conclusion is that the power-law clustering observed in many vegetation ecosystems may simply be an aggregation effect and the exponential truncation observed when there is increased stress is due to an increase in the linear death rate of clusters.

2. Theory

The idea developed here is to model the patches themselves as opposed to an individual spatial site as is done in probabilistic cellular automata [19, 20]. We denote $c_k(t)$ as the density of patches of size k at time t, where time is taken to be continuous. A continuous model of patch-sizes can be studied, however for the present k shall take positive integer values only, $k \in \{1, 2, \ldots\}$. A kernel of aggregation gives the rate at which patches of size i and j aggregate together to form a patch of size $i + j$, this kernel is denoted $K(i, j)$. Finally it is assumed there is a constant rate at which patches of size 1 or monomers enter the system. These assumptions are general and can include many different phenomena, including static clusters and diffusing monomers [18]. The governing master equation, also known as

the Smoluchowski equation [21] is then

$$\frac{\mathrm{d}}{\mathrm{d}t}c_k = \frac{1}{2}\sum_{i+j=k} K(i,j)c_i c_j - \sum_{j\geq 1} K(j,k)c_j c_k + \delta_{k,1}, \tag{1}$$

where $\delta_{k,1}$ is the Kronecker-delta function that is 1 when $k = 1$ and 0 otherwise. For convenience, time has been re-scaled such that the rate at which aggregation occurs is 1. It is instructive to imagine a single unit or monomer coming into contact with a cluster and calculating the rate at which this occurs for larger as opposed to smaller clusters. If $a > 0$ then, assuming the size of the monomer is negligible, the monomer rate equation is $K(i) = i^{-a}$. This means smaller clusters are favoured and the growth rate reduces as clusters grow larger in size. An ecological explanation of this could be due to the self-limitation through competition a larger cluster experiences with itself, thus reducing its potential for growth. Smaller clusters have more space and thus can grow at a quicker rate.

When $a < 0$, larger clusters are favoured for growth compared with smaller clusters, this can be seen as a form of the Allee effect [22]. In the regime when $a < 0$, small clusters are more susceptible to environmental perturbation and as such, have a lower propensity for growth. At the other length scale, larger clusters of vegetation are able to regulate their environment more and thus have greater resources for growth (An example species where this holds is ribbed mussels [23], where larger clusters provide protection and shelter for new mussels). This example of an Allee effect can be demonstrated by again considering the rate at which single units of vegetation aggregate to a cluster. If a $i > j$, then $K(1,i) = 1 + i^{-a} > 1 + j^{-a} = K(1,j)$ i.e. the rate at which a larger patch recruits new growth is greater than for a smaller patch. A value for a then can give an indication of whether there is strong small cluster growth at the expense of large clusters forming or if the converse holds.

An alternative explanation of the aggregation exponent a is due to the edge effects of a cluster. A single individual vegetation unit aggregates to a cluster proportional to the edge of that cluster. If all clusters are non-fractal then it would be expected that a vegetation unit aggregates at rate $i^{1/2}$, since the length of a non-fractal object scales as a square root with its area. For a general fractal cluster with boundary dimension d, it would be expected that an individual unit scales as $i^{1/d}$.

Various properties are desirable for the kernel. Firstly symmetry, where the rate at which patches of size i and j aggregate does not depend on the

ordering of the patches i.e. $K(i,j) = K(j,i)$. Secondly, scaling homogeneity, where the rate at which patches of a certain size aggregate scales by some factor $K(mi, mj) = m^{\lambda}K(i,j)$. The simplest kernel that satisfies these conditions is the constant kernel $K(i,j) = 1$, corresponding to the case where $\lambda = 0$. When this form of kernel is assumed, the tail-solution (for large k) has the simple form [24]

$$c_k \sim \frac{1}{\sqrt{4\pi}} \frac{1}{k^{3/2}}. \tag{2}$$

The tail of the patch-size distribution is a power law with exponent 3/2, where the power law nature of the solution is a consequence of the injection term (where births of patch size one enter the system) and the non-linear aggregation term in the equation. The equation can be solved analytically for more general kernels of the type

$$K(i,j) = i^{-a} + j^{-a}. \tag{3}$$

This type of kernel also admits an analytic solution in the large patch-size limit [25, 26] with a steady state distribution of the form where

$$c_k \sim Ck^{-\tau} \tag{4a}$$

$$\tau = \frac{3-a}{2}, \quad C = \sqrt{\frac{1-a^2}{4\pi} \cos\left(\frac{\pi a}{2}\right)}. \tag{4b}$$

For a steady state to exist we require $-1 < a < 1$ and hence the scaling exponent can be found on the interval $\tau \in (1,2)$. The dynamics of the equation can be assessed by defining the cross-over time, which is the time taken for a density of patches of a certain size to reach its asymptotic value. The cross-over time for a patch of size k_* to the steady state solution c_{k_*} is found to take the form $t = (k_*)^z$ where $z = (1+a)/2$. The scaling of the cross-over time and the patch-size exponent can be related by the simple linear equation $\tau = 2 - z$. This gives a linear relationship between the static exponent at stationarity and its dynamic exponent.

A real vegetation system is not purely defined by an aggregation process however. In particular in the previous example there is no death either of single vegetation units or patch clusters. Death may lead to changes in the exponent of the stationary distribution and so it is important to include in any model of vegetation clustering. It is also assumed that a death event does not lead to fragmentation of the cluster. A modified Smoluchowski equation

with a linear death term can then be produced as

$$\frac{\mathrm{d}}{\mathrm{d}t}c_k = \frac{1}{2}\sum_{i+j=k} K(i,j)c_i c_j - \sum_{j\geq 1} K(j,k)c_j c_k + \mu(k+1)c_{k+1} - \mu(k)c_k, \quad (5a)$$

$$\frac{\mathrm{d}}{\mathrm{d}t}c_1 = -\sum_{j\geq 1} K(j,1)c_j c_1 + 1 + \mu(2)c_2 - \mu(1)c_1. \quad (5b)$$

The general additive aggregation kernel is again taken to be of the form $K(i,j) = i^{-a} + j^{-a}$, where a represents the scaling parameter of the rate at which aggregates of a certain size join. If it is equally likely for a cluster of a certain size to aggregate with a cluster of any other size then the scale parameter $a = 0$. For a pure aggregation system with no fragmentation, this leads to a cluster scaling of 3/2. $\mu(k)$ defines the death rate, which is the rate at which individual units are lost from a patch, where a patch of size k transitions to a patch of size $k-1$ due to exogenous or endogenous factors. A number of different forms of this death rate may be considered dependent on the biological details of the system. For example if each individual has a constant rate of death regardless of the size of patch its contained, such as due to lack of rainfall or grazing, is then $\mu(k) = \mu k$. If death occurs at the edge of a patch then the death rate is $\mu k^{1/d}$, where d is the boundary dimension of the patches. The simplest form of the death rate is where $\mu(k) = \mu$ for all k. In order to gain insight into the effect of a death rate on the resulting patch-size distribution, we assume the final form of the death rate.

In order to gain analytic tractability on the model a constant aggregation kernel is assumed ($a = 0, K = 2$) together with a constant death rate for each individual within a patch. The strategy for deriving a solution is similar to the strategy in Krapivsky et al. [26]. A constant kernel $K(i,j) = 2$ is used. Eq. (5) is rewritten as

$$\frac{\mathrm{d}}{\mathrm{d}t}c_k = \sum_{i+j=k} c_i c_j - 2c_k \sum_{j\geq 1} c_j + \mu c_{k+1} - \mu c_k, \quad (6a)$$

$$\frac{\mathrm{d}}{\mathrm{d}t}c_1 = -2c_1 \sum_{j\geq 1} c_j + 1 + \mu c_2 - \mu c_1. \quad (6b)$$

The asymptotic tail of the resulting patch-size distribution is then sought in order to gain an understanding of how the linear death rate affects the stationary distribution. By using the asymptotic approximation and assuming k is large, the k-th coefficient in this expansion and hence the density of

patches of size k is

$$c_k = k^{-3/2} \exp(-\Lambda k), \tag{7}$$

where $\Lambda = \log(1 + \mu N)$ and N is the total population size (See Appendix A for a derivation). The solution is therefore a power law with an exponential truncation of factor Λ. When the death rate is 0, $\Lambda = 0$ and hence the patch-size distribution is a pure power law as is expected. A large death rate will lead to a solution that is dominated by an exponential decay term, hence the patch-size distribution is expected to have a smooth transition from a pure power law to an exponential distribution. A dimensionality argument of Eq. 6 [27] also leads to a power law exponent of the form 3/2. This solution can be compared to the general power-size distribution with exponential cut-off $N(k)$ given by

$$N(k) = Ck^{-\alpha} \exp(-k/k_x), \tag{8}$$

where k_x is the patch-size above which $N(s)$ decreases faster than power-law [2]. Matching terms and assuming μN is small gives the following simple relationship between the cross-over patch size k_x and death rate μ as

$$k_x = \frac{1}{N\mu}. \tag{9}$$

The model therefore predicts an inverse relationship between patch-size cross-over and death rate. This also predicts that when the death rate is small enough, the cross-over patch-size k_x may be larger than the system size and as such the exponential tail may not be observed in empirical distributions.

3. Results

In order to compare the model predictions of patch formation in an aggregation system with a constant death rate to the prediction of the patch-size distribution obtained in Eq. 7 is compared to a simple probabilistic cellular automata model of vegetation growth. The cellular model is similar to the one discussed in [11], the model is defined on a toroidal lattice where each site can exist in one of two states: occupied (1) and empty (0). The occupied state propagates through nearest neighbour growth at rate β, as well as through a background constant birth probability γ. The alive sites transition to a dead site with a constant death probability μ. Hence if n_x is the number of alive sites in the neighbourhood of site x, the transitions can

be summarised as

$$P_x(0 \to 1) = \epsilon \min\{1, \gamma + \beta n_x/4\}, \tag{10a}$$
$$P_x(1 \to 0) = \epsilon\mu, \tag{10b}$$

where ϵ sets the total reaction rate of the system and was implemented to reduce the probability of multiple events occurring within the same neighbourhood. The minimum function is used here to guarantee the probability of transitioning to an alive state is one in the rare case when the sum of the two probabilities increases above one.

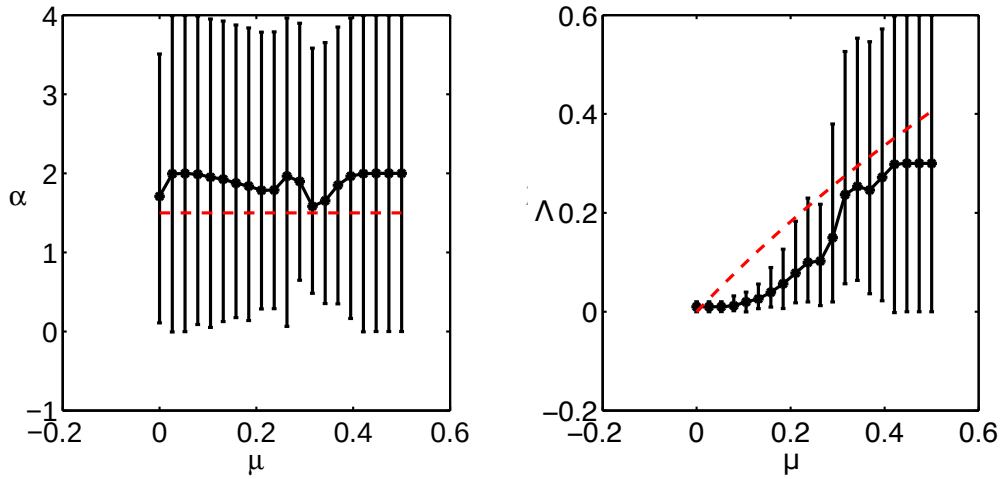
Simulations were conducted for constant local growth, birth rate and reaction rate $\beta = 0.2, \gamma = 0.01, \epsilon = 0.1$ and over a range of death rates. Simulations were ran for lattice length $L = 500$ and for 1000 replicates of each parameter set. The patch-size distribution was recorded for each simulation run after 600 time-steps. This was chosen so that when $\mu = 0$, the lattice is approximately 50% occupied. The following power-law with exponential truncation was fitted to the distribution using a maximum likelihood method

$$f(K = k) = Ck^{-\alpha} \exp(-\Lambda k), \tag{11}$$

for some normalising factor C. The resulting maximum likelihood estimators were found using a downhill simplex method implemented in Matlab R2014a [28]. The approximate solution to the aggregation equation predicts a constant power-law exponent α of 3/2. This is close to the inferred value from simulation for the range of μ values studied (Fig. 1a). The exponential factor Λ is zero when the death rate is zero (Fig. 1b), as predicted. For increasing death rate, Λ increases again as predicted. Overall there is an increase in the exponential factor for increasing death rate as is predicted, however the functional form of the increase is not fully captured by the mean field approximation.

4. Discussion

Changing the focus away from explicit spatial modelling of vegetation patch formation and instead focusing on the dynamics of patch-sizes gives a unique insight into the underlying aggregation-fragmentation processes. Here we have primarily focused on solutions to equations where the aggregation kernel that governs the rate at which patches of two sizes will aggregate by



(a) comparison of power-law exponent from simulation to theoretical prediction

(b) comparison of exponential factor from simulation to theoretical prediction

Figure 1: Exponents of patch-size distribution compared to simulations. Theoretical values shown as red dashed lines, while simulation calculated values are given as black dots with 95% confidence intervals. The theoretical values for the power-law exponent α and the exponential factor Λ are derived in Eq. 7. As predicted for small values of the death rate the power-law component of the patch-size distribution is constant whilst there is an increase in the exponential component for increasing death rate.

either a constant or power law kernel. For a system where there is aggregation only the resulting patch-size distribution is that of a pure power law, with exponent that is dependent on the exponent of the power law aggregation kernel. The introduction of a linear death term, where an individual is lost from a patch at rate μ/k gives rise to a power law with exponential tail distribution of the form $c_k \sim k^{-\alpha} \exp(-\Lambda k)$. This solution holds generally when there is a linear death term and power-law aggregation kernel, even when the kernel is composed of a sum of two power-laws. Further, α is dependent on the specifics of the aggregation term alone and Λ is dependent on the death rate alone. This separation of the aggregation and fragmentation term implies, in principle, the ability to infer aggregation and death processes through observing the converged patch-size distribution alone, hence this is applicable to inferring process from a single spatial snapshot.

Kéfi et al. [6, 2] predicts that a power-law distribution in the patch-size distribution occurs when a global environmental death rate is small. This transitions to an exponential distribution when there is greater stress on the system through this global death rate term. The model used is a spatially-explicit one with a local growth term and a background death rate. The model proposed in this article can be seen as a deterministic equivalent of this spatially-explicit model. Through the derived solution in this article it is observed that there should always be an exponential tail to the distribution if the death rate is non-zero. Similar arguments have also been made recently [29], but notably none have explained the origin of a power law with exponential tail observed in vegetation systems. The derived model then, provides a theoretical origin to the observed spatial patterns in vegetation ecosystems that are under a pressure that can be considered constant throughout space (rainfall, grazing etc.). As an example, if all sites had the same death rate regardless of its neighbourhood, such as for a grazer, the death rate would be μk for a patch of size k. The model also suggests that a power-law with exponential tail is a more accurate description of the patch-size distribution, although when the death rate is small, the exponential tail may not be observed directly. This approach would be able to provide further insights into the nature of the patch-size distribution for other systems where disturbance may be spatially distributed.

The model also gives insight into how there can be a continuous array of power-law exponent observed in nature. The aggregation with no death model predicts that power-laws exponents in the range $(1, 2)$ are physically possible, which is what has been observed in a number of ecosystems [7, 6, 8]. The model predicts that a change in the exponent of a patch-size distribution is related to a change in the power-law exponent of the aggregation kernel. A simple dimensionality argument can be used to show that in the aggregation and death model with a kernel that has a general power law scaling as described in Eq. 3, the resulting stationary distribution will have the same exponent as that in the model with no death [27]. The conclusion of how to relate the patch-size distribution to the system dynamics is that both the power-law exponent and the presence of an exponential cut-off does give an indication of the underlying dynamics. More complex fragmentation processes than the one discussed would alter these conclusions however, as a non-linear fragmentation process will also lead to self-similar solutions and thus the two processes are confounded when only the stationary state is observed [30], such processes include storms and other strong weather events

that could split a single cluster of vegetation into multiple clusters. The size of the system where the dynamics occur, such as in the lattice model, may also have an impact on the exponents of the patch-size distribution due to finite-size effects [31].

Other possible extensions to the model could include multi-species systems, where patches are formed of multiple species each with their own intrinsic death rates. Multi-species systems have already been considered in the physical sciences and as such this would make for an interesting avenue of future research [32]. Where the aggregation process is indistinguishable between two different species, this leads to similar results laid out in this article [33]. However, more complex interactions such as inter-specific competition would inevitably lead to a more complex relationship between the exponent death term and the underlying death rates. The model equations were scaled such that the rate of aggregation and rate at which single vegetation units are created is one. This was done for convenience since we were interested in studying the scaling alone, whereas these parameters change the constant of the patch-size distribution only. Another extension then would be to explicitly calculate the constant for the patch-size distribution and study how this changes as the other system rates change.

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Appendix A. Derivation of asymptotic solution

A moment-generating function is used to find the steady state solution to this equation in a similar fashion to the one described in Krapivsky et al. [26]. Firstly define the total number of all patches as $N = \sum_{k\geq 1} c_k$ and then sum Eq. (6a-b) in order to obtain

$$\frac{dN}{dt} = \sum_{k\geq 1}\sum_{i+j=k} c_i c_j - 2\sum_{k\geq 1} c_k \sum_{j\geq 1} c_j + 1 + \sum_{k\geq 1} \mu c_{k+1} - \sum_{k\geq 1} \mu c_k, \tag{A.1}$$

$$\frac{dN}{dt} = N^2 - 2N^2 + 1 - \mu c_1, \tag{A.2}$$

$$\frac{dN}{dt} = -N^2 + 1 - \mu c_1. \tag{A.3}$$

Dynamically, consider when N is at equilibrium. If $\mu = 0$ then the stationary solution is $N = 1$. If $\mu > 0$ then the equilibrium solution is necessarily bounded between one and zero as N and c_1 are always positive.

The moment-generating function $C(z,t) = \sum_{k=1}^{\infty} c_k z^k$ is now considered. Multiplying Eq. (6) by z^k and summing over all k gives the following

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}C &= C^2 - 2NC + z + \mu\sum_{k\geq 1} z^k c_{k+1} - \mu\sum_{k\geq 1} z^k c_k \\ &= C^2 - 2NC + z + \frac{\mu}{z}C - \mu C - \mu c_1. \end{aligned} \tag{A.4}$$

The C^2 term is derived using the relationship

$$\left(\sum_{k\geq 1} a_k\right)^2 = \left(\sum_{i\geq 1} a_i\right)\left(\sum_{j\geq 1} a_j\right) = \sum_{k\geq 1}\sum_{i+j=k} a_i a_j. \tag{A.5}$$

The new moment generating function defined as $A(z,t) = C(z,t) - N(z,t)$ is considered in order to derive the final stationary solution. The time derivative is calculated by combining Eq. A.4 with Eq. A.3

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}A(z,t) &= \frac{\mathrm{d}}{\mathrm{d}t}C(z,t) - \frac{\mathrm{d}}{\mathrm{d}t}N(t) \\ &= C^2 - 2NC + \frac{\mu}{z}C + z - \mu C - \mu c_1 - 1 + N^2 + \mu c_1 \\ &= A^2 + \frac{\mu}{z}C - \mu C + z - 1 \\ &= A^2 + \mu\frac{1-z}{z}A + \mu\frac{1-z}{z}N + z - 1. \end{aligned} \tag{A.6}$$

Note that the right-hand side is quadratic in terms of A. Setting the time-derivative to zero gives the steady-state solution of the moment-generating function as

$$A = \mu\frac{z-1}{z} + \sqrt{\mu^2\frac{(1-z)^2}{z^2} - 4\left(\mu\frac{1-z}{z}N + z - 1\right)}. \tag{A.7}$$

In order to proceed it is assumed that the death rate μ is small and only the leading order term is kept. Hence

$$A \approx 2\sqrt{1 - z - \mu\frac{1-z}{z}N}. \tag{A.8}$$

The strategy is to find A in terms of the power series $\sum_{k=1}^{\infty} c_k z^k$, where c_k is a function of μ. Assuming z is sufficiently close to one such that $z + \mu(1 - z)N/z < 1$, the expansion of $\sqrt{1-x}$ is used to obtain

$$A_{\text{approx}} = 2\sum_{k=0}^{\infty} \frac{\Gamma(3/2)}{\Gamma(3/2-k)\Gamma(k+1)} (1+\mu N)^{1/2-k} \left(-z - \mu N/z\right)^k . \quad \text{(A.9)}$$

Using the relationship $\Gamma(z)\Gamma(1-z) = \frac{\pi}{\sin(\pi z)}$, cancelling the $(-1)^k$ terms and absorbing all constants into a constant c term

$$A_{\text{approx}} = c\sum_{k=0}^{\infty} \frac{\Gamma(k-1/2)}{\Gamma(k+1)} (1+\mu N)^{1/2-k} \left(z + \mu N/z\right)^k . \quad \text{(A.10)}$$

Using the binomial expansion, this becomes

$$A_{\text{approx}} = c\sum_{k=0}^{\infty}\sum_{i=0}^{k} \frac{\Gamma(k-1/2)}{\Gamma(k+1)} \frac{\Gamma(k+1)}{\Gamma(i+1)\Gamma(k-i+1)} (1+\mu N)^{1/2-k} (\mu N)^{k-i} z^{2i-k}. \quad \text{(A.11)}$$

In order to find the k-th coefficient as $k \gg 1$ the leading order of the i term in the binomial is considered. Given that $\mu N \ll 1$, the i dependent terms are dominated by $i = k$. Hence the kth term of the expansion where k is large is

$$c\frac{\Gamma(k-1/2)}{\Gamma(k+1)} (1+\mu N)^{1/2-k} z^k. \quad \text{(A.12)}$$

By using the asymptotic approximation $\Gamma(n+a)/\Gamma(n) \sim n^a$ and assuming k is large, the k-th coefficient in this expansion and hence the density of patches of size k is

$$c_k = ck^{-3/2} \exp(-\Lambda k), \quad \text{(A.13)}$$

where $\Lambda = \log(1 + \mu N)$.

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